

INHERITANCE OF FRUIT-LENGTH IN CAPSICUM

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INTRODUCTION

THE work of Halsted (1914, 1915 and 1916) indicates that quantitative characters in *Capsicum* follow the multiple-factor rule for size inheritance. Halsted figures F_2 progenies of the cross Golden Queen $\times$ Red Cluster showing continuous variation in the size and shape of the fruits. He found that an F_2 progeny of nearly a thousand individuals did not fully reproduce either parent.

* Paper from the Department of Botany of the University of Michigan, No. 292.

MATERIALS AND METHODS

The present study was limited to a single character, the length of the fruit, and for this purpose two varieties of hot peppers, Coral Gem Bouquet and Anaheim, were used. The differences between these types are shown in the accompanying illustrations (Pl. XXXII). Both varieties have elongate slender fruits, although the Anaheim is much the larger in all respects. The mean length of Coral Gem was 23.2 mm. while that of Anaheim was 156.9 mm. By the use of such types it was hoped that complicating factors due to extreme differences in the shape of the

TABLE I
VARIATION IN FRUIT-LENGTH OF CORAL GEM PEPPER
GROWN IN DIFFERENT YEARS

Class value in mm.	1923	1926	Total
14	2		2
15	1	4	5
16	3	4	7
17	3	11	14
18	11	14	25
19	11	40	51
20	23	44	67
21	23	64	87
22	50	72	122
23	67	77	144
24	69	67	136
25	85	46	131
26	52	25	77
27	59	23	82
28	21	5	26
29	13	4	17
30	5		5
31	1		1
32	0		0
33	1		1
Total	500	500	1000
Mean	24.1	22.4	23.2



FIG. 1. The Coral Gem parent



FIG. 2. The Anaheim parent



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fruits could be eliminated and, as the peppers were easy to grow, the production of large progenies offered ample material for a study of the inheritance of the factors for length. All measurements were to the nearest mm.

The seed used were from commercial sources. Both the original parent generations and the later self-pollinated generations of the parents bred true.

EXPERIMENTAL WORK

Variation in the parents

Table I shows the variation in the length of the Coral Gem pepper grown in two different years. Five hundred fruits were measured in each year. The mean length for the two years differed by 1.7 mm. The mean length of the Coral Gem parent is taken as the mean of both years. Table II gives like data for the Anaheim parent grown in four different years. There is considerable variation in the length of the Anaheim from year to

TABLE II

VARIATION IN FRUIT-LENGTH OF ANAHEIM PEPPER
GROWN IN DIFFERENT YEARS

Class value in mm.	1923	1924	1925	1927	Total
100-109	1				1
110-119	5		2		7
120-129	0		3	2	5
130-139	1	3	8	33	45
140-149	6	8	8	89	111
150-159	18	18	17	109	162
160-169	33	4	28	27	92
170-179	17	8	42	5	72
180-189	7	2	18		27
190-199	2		3		5
200-209	1		1		2
Total	91	43	130	265	529
Mean	162.5	157.8	165.7	150.3	156.9

year. In 1925, for example, 139 fruits had a mean length of 165.7 mm. while in 1927 the mean length of 265 fruits was 150.3 mm. The records show, however, that the fruits measured in 1925 came from 52 plants, an average of 2.7 fruits per plant, while the fruits measured in 1927 came from 53 plants, an average of 5 fruits per plant. The plants grown in 1927 probably averaged at least 6 fruits each although only 5 were measured. In 1925 all the available fruits were measured. It seems probable that the normal seasonal variation plus the heavier set of fruits for 1927 accounts for the difference in the mean length of the Anaheim for these years. It should also be observed that the number of fruits measured in any one year was not large. The heavier set of fruit in the last year was presumably due to the weather conditions which prevailed at the time of pollination. If the mean of the Anaheim parent be taken by combining the data for the four years, it is 156.9 mm.

TABLE III

VARIATION IN FRUIT-LENGTH OF F_1 HYBRIDS BETWEEN
CORAL GEM AND ANAHEIM

Class value in mm.	1923		1925		Total
	Anaheim × Coral Gem	Coral Gem × Anaheim	Anaheim × Coral Gem	Coral Gem × Anaheim	
33-37			4	4	8
38-42		1	14	6	21
43-47	6	5	54	29	94
48-52	18	19	107	106	250
53-57	49	42	177	172	440
58-62	125	109	101	116	451
63-67	172	172	35	53	432
68-72	104	111	7	14	236
73-77	24	31	1		56
78-82	2	9			11
83-87		1			1
Total	500	500	500	500	2000
Mean	63.6	64.3	54.2	55.7	59.4

The F₁ generation

Table III shows the variation in the F₁ hybrids of Coral Gem and Anaheim. The difference between the F₁ generations grown in 1923 and 1925 amounts to 9.0 mm. or 16 per cent of the F₁ mean for 1925. The reciprocal crosses are, however, consistent, the differences between them being 0.7 mm. in 1923 and 1.5 mm. in 1925, and the variation, though rather extreme, appears to have been due to seasonal conditions alone. By combining the F₁ data for the two years the mean is found to be 59.4 mm.

TABLE IV

VARIATION IN MEAN FRUIT-LENGTH OF F₂ PLANTS
(10 FRUITS PER PLANT) OF CROSSES BETWEEN
CORAL GEM AND ANAHEIM

Class Value in mm.	1924		1925		Total
	(Coral Gem × Anaheim) Selfed	(Anaheim × Coral Gem) Selfed	(Coral Gem × Anaheim) Selfed	(Anaheim × Coral Gem) Selfed	
23-27		1			1
28-32		2	4	6	12
33-37	4	2	9	9	24
38-42	11	10	13	10	44
43-47	17	18	27	16	78
48-52	24	19	20	9	72
53-57	34	16	31	13	94
58-62	34	18	27	13	92
63-67	27	13	15	7	62
68-72	20	14	15	6	55
73-77	19	14	4	2	39
78-82	13	5	7	3	28
83-87	9	5	3	1	18
88-92	3	4	1	4	12
93-97	1	3		0	4
98-102	3	2		0	5
103-107		1		1	2
108-112		2			2
Total	219	149	176	100	644

Mean = 58.6 Skewness = 0.53

The F₂ generation

Table IV gives the variation in the F₂ generation for two successive years. In the parent and F₁ generations data were obtained by measuring mass collections from each family. This procedure could not be followed in the generations involving segregation, since the segregating units were not individual fruits but plants. It was necessary in such cases to determine a mean length of fruit for each plant. In the F₂ generation 10 fruits per plant were measured. Thus the 644 individuals of the F₂ generation represent a total of 6440 measured fruits. The mean of F₂ was 58.6 mm.

Discussion of variation in F₁ and F₂

The means of the Coral Gem and Anaheim parents were respectively 23.2 and 156.9 mm. and the arithmetic mean of the two was 90.0 mm. The mean of the F₁ was 59.4 mm. or 30.6 mm. less than the mean of the parents. As a rule, divergence of the F₁ from the mean of the parents is attributed to dominance and in the present case it would seem that the smaller parent was to a considerable extent dominant over the larger. A very different explanation is that in the inheritance of quantitative characters the hereditary factors have a proportionate rather than an absolute effect. This hypothesis of the proportionate effect of quantitative factors is given in detail by Zeleny (1922) in his studies of eye facet number in *Drosophila*. Earlier studies, Seyster (1919) and Krafka (1920), showed that in both bar and ultra-bar the eye facet number decreased with increase in the temperature at which the larvae were grown. On an average a decrease in temperature of one degree Centigrade gave an increase of 10 per cent in facet number. The effect of a change in temperature was thus proportional to the mean of the stock, those with low mean values giving smaller effects while those with high mean values gave greater effects. Zeleny reasoned that germinal factors would produce an effect similar to that produced by temperature. He says: "It is a common principle of embryology that a changed condition does not act by accretion, i.e. by the addition or subtraction of individual parts without

affecting the rest. On the contrary, the action is upon all the pre-existing parts of the organ. The result then depends not only upon the strength of the new agent, but also upon the reaction capacity of these pre-existing parts. Since a new factor, f , acts upon the whole complex, the value of the pre-existing mechanism, m , is a factor in the result as well as f . This general statement applies to both germinal and environmental factors."

An important consequence of the theory of proportionate effect of the factors is that a population which has a normal distribution of the factors will usually give a skewed curve if the data are arranged in the customary equal-size classes. In other words, a skewed curve is the normal expectation for such a distribution. The analysis of such data should, as Zeleny has pointed out, be based upon the logarithmic mean and the dispersion of the logarithms of the measurements. Inasmuch as the factors are assumed to have a proportionate effect, it becomes necessary to vary the class ranges accordingly. If throughout the entire range of variation the size of each class is made a certain fixed per cent of its own mean, all the classes will then have the same logarithmic range. They will be factorially equal and a population having a normal distribution of the factors should, when treated in this way, give a normal curve. Zeleny's analysis of variation in facet number is based upon logarithmic distributions.

There seems to be no question but that the type of distribution based upon logarithmic classes gives a more suitable means of representing the effects of temperature upon eye facet number in bar-eye stocks of *Drosophila*, than does a distribution based upon equal-size classes. There is a very strong a priori presumption that the same thing holds true of genetic factors. The fact that growth phenomena are of a geometric order makes it probable that the changes produced by genetic factors would also be proportionate effects and thus conform to a logarithmic distribution.

It has been pointed out in discussing the pepper data that the wide departure of the F_1 mean from the arithmetic mean of the parents might be explained in two very different ways: (1) on the theory of partial dominance on the part of the small parent; and (2) on the theory that the factors for length have a propor-

tionate effect. If the latter theory is correct we should expect the F_1 mean to approximate not the arithmetic mean of the parents but their logarithmic mean. Since the F_1 mean was 59.4 mm. and the logarithmic mean of the parents was 60.3 mm. the expectation is verified. If, however, it were assumed that dominance accounted for the difference between the F_1 and the arithmetic mean of the parents, it would be a remarkable coincidence that the degree of dominance should have been such as to give an F_1 mean so nearly identical with the logarithmic mean of the parents.

If the effects of the factors are proportionate, the mean of the F_2 generation, as well as that of the F_1 , would be expected to conform to the logarithmic mean of the Coral Gem and Anaheim parents. The F_2 mean was 58.6 mm., a difference of only 1.7 mm. from the logarithmic mean of the parents and again the expectation is realized. The variation in F_2 was continuous, with no indication of bi- or multi-modal distribution. Theoretically the F_2 generation should reproduce the parent types. There were 644 progeny in the F_2 with a range of 85 mm. The inter-parental range was 133 mm. Thus the range of F_2 was only 64 per cent of the parent range.

It was pointed out earlier that, if the factors have a proportionate effect, the logarithmic distribution of a population segregating for length factors should give a normal curve, or at all events, a more nearly normal curve than the same population when arranged in equal-size classes. Table VII gives the F_2 data arranged in logarithmic classes. It is clear that the distribution here is much more nearly normal than when the same data are grouped in equal-size classes (Table IV). Calculating the skew-

ness of the two distributions by the formula $\alpha_3 = \frac{\mu_3}{\sigma^3}$ we have

	Equal-size classes	Logarithmic classes
$\alpha_3 F_2$	0.53 ± 0.07	-0.08 ± 0.07

The skewness of the logarithmic distribution is only slightly greater than the probable error, while the skewness of the arith-

TABLE V

VARIATION IN MEAN FRUIT-LENGTH OF BACK-CROSS
PLANTS (20 FRUITS PER PLANT) IN BACK-CROSSES
BETWEEN CORAL GEM AND F_1

Class value in mm.	Coral Gem $\times F_1$	$F_1 \times$ Coral Gem	Total
23-27	7	20	27
28-32	31	57	88
33-37	51	62	113
38-42	48	56	104
43-47	39	23	62
48-52	25	6	31
53-57	11	1	12
58-62	1		1
Total	213	225	438

Mean = 37.6 Skewness = 0.37

TABLE VI

VARIATION IN MEAN FRUIT-LENGTH OF BACK-CROSS
PLANTS (5 FRUITS PER PLANT) IN BACK-CROSSES
BETWEEN ANAHEIM AND F_1

Class value in mm.	Anaheim $\times F_1$	$F_1 \times$ Anaheim	Total
50-59	1		1
60-69	2	1	3
70-79	9	1	10
80-89	26	15	41
90-99	28	14	42
100-109	27	12	39
110-119	23	11	34
120-129	12	11	23
130-139	3	3	6
140-149	1	2	3
150-159	0		0
160-169	1		1
170-179	1		1
Total	134	70	204

Mean = 102.6 Skewness = 0.53

metic distribution is more than seven times the probable error. It can scarcely be doubted that the difference is significant and that the absence of skewness in the logarithmic curve indicates that the factors have a proportionate effect.

The Back-crosses

In the back-cross between the F_1 and the Coral Gem parent (Table V) the gametes produced by the Coral Gem would all be identical. The gametes produced by the F_1 would, on the other hand, vary from pure Coral Gem to pure Anaheim. Thus the back-cross progeny would be expected to range from the F_1 to the Coral Gem in size and the mean of the progeny should agree with the logarithmic mean of the F_1 and Coral Gem. As the mean of the back-cross was 37.6 mm. and the logarithmic mean of the parents was 37.1 mm., the agreement is extremely close, the difference being 0.5 mm.

In the same way the back-cross between the F_1 and Anaheim (Table VI) should give a progeny whose mean would conform to the logarithmic mean of the parents. The mean of the back-cross was 102.6 mm. while the logarithmic mean of the parents was 96.5 mm. The difference amounts to 6.1 mm. or 6 per cent of the mean of the back-cross. While this difference is greater than might have been expected, it could well be the result of seasonal variation.

The variation in the back-crosses like that of the F_2 was continuous and gave no indication of a bi- or multi-modal character. And also, as in the case of the F_2 , the back-cross data in logarithmic classes (Tables VIII and IX) showed much less skewness than when grouped in equal-size classes (Tables V and VI). The data on skewness are summarized below:

Back-cross	Type of distribution	Skewness
$F_1 \times$ Coral Gem	arithmetic	0.37 ± 0.08
$F_1 \times$ Anaheim	"	0.53 ± 0.12
$F_1 \times$ Coral Gem	logarithmic	0.05 ± 0.08
$F_1 \times$ Anaheim	"	0.11 ± 0.12

TABLE VII

LOGARITHMIC DISTRIBUTIONS OF MEAN FRUIT-LENGTHS
OF F₂ PLANTS (10 FRUITS PER PLANT) OF CROSSES
BETWEEN CORAL GEM AND ANAHEIM
Width of logarithmic classes 0.05

Class value in mm.	1924		1925		Total
	$\left(\begin{smallmatrix} \text{Coral Gem} \\ \times \\ \text{Anaheim} \end{smallmatrix} \right)_{\text{Selfed}}$	$\left(\begin{smallmatrix} \text{Anaheim} \\ \times \\ \text{Coral Gem} \end{smallmatrix} \right)_{\text{Selfed}}$	$\left(\begin{smallmatrix} \text{Anaheim} \\ \times \\ \text{Coral Gem} \end{smallmatrix} \right)_{\text{Selfed}}$	$\left(\begin{smallmatrix} \text{Coral Gem} \\ \times \\ \text{Anaheim} \end{smallmatrix} \right)_{\text{Selfed}}$	
25.1-28.1		1			1
28.2-31.5		1	2	4	7
31.6-35.4	2	2	5	5	14
35.5-39.7	9	7	14	10	40
39.8-44.6	6	11	19	11	47
44.7-50.0	32	27	25	16	100
50.1-56.1	37	14	31	12	94
56.2-63.0	42	27	39	21	129
63.1-70.7	37	14	21	9	81
70.8-79.3	31	24	13	6	74
79.4-89.0	17	11	7	2	37
89.1-99.9	4	5		3	12
100.0-112.2	2	5		1	8
Total	219	149	176	100	644

Skewness = - 0.08

The arithmetic distribution of the data from the back-cross to Coral Gem gives a value for skewness amounting to more than four times the probable error, while the skewness of the logarithmic distribution for the same data is less than the probable error. The skewness of the arithmetic distribution of the data from the back-cross to Anaheim is again more than four times the probable error, whereas the skewness of the logarithmic distribution is, as before, less than the probable error. Thus the back-cross generations and the F₂ behave alike with respect to skewness, and it becomes increasingly probable that the theory of proportionate effects is the correct one.

The mean fruit-length of the back-cross progenies was based upon 20 measurements per plant in the back-crosses with Coral

TABLE VIII

LOGARITHMIC DISTRIBUTIONS OF MEAN FRUIT-LENGTHS
OF BACK-CROSS PLANTS (20 FRUITS PER PLANT) IN
BACK-CROSSES BETWEEN CORAL GEM AND F_1

Width of logarithmic classes 0.05

Class value in mm.	Coral Gem $\times F_1$	$F_1 \times$ Coral Gem	Total
22.4-25.0	1	7	8
25.1-28.1	9	22	31
28.2-31.5	18	37	55
31.6-35.4	41	51	92
35.5-39.7	42	50	92
39.8-44.6	50	41	91
44.7-50.0	31	15	46
50.1-56.1	18	2	20
56.2-63.0	3		3
Total	213	225	438

Skewness = - 0.05

TABLE IX

LOGARITHMIC DISTRIBUTIONS OF MEAN FRUIT-LENGTHS
OF BACK-CROSS PLANTS (5 FRUITS PER PLANT) IN
BACK-CROSSES BETWEEN ANAHEIM AND F_1

Width of logarithmic classes 0.05

Class value in mm.	Anaheim $\times F_1$	$F_1 \times$ Anaheim	Total
50.1-56.1	1		1
56.2-63.0	1		1
63.1-70.7	1	1	2
70.8-79.3	9	1	10
79.4-89.0	26	15	41
89.1-99.9	28	14	42
100.0-112.2	37	17	54
112.3-125.8	23	13	36
125.9-141.2	5	8	13
141.3-158.4	1	1	2
158.5-177.8	2		2
Total	134	70	204

Skewness = - 0.11

Gem and upon 5 measurements per plant in the back-crosses with Anaheim. The reason for this difference was that in the latter case the fruits were much larger and fewer were produced upon a single plant.

The Second Generation after the Back-crosses

Tables X and XI give the distributions in arithmetic and logarithmic classes for the various families of the second generation after back-crossing. The 28 families of these tables were derived from selfed plants of the back-cross generation whose mean length of fruits ranged from types as small as the Coral Gem to others as large as the F_1 . Each individual represents the mean of 20 measured fruits from a single plant. The outstanding feature of the tables is the unimodal character of the distributions, there being scarcely a suggestion of discontinuous variation. In this respect the distributions agree with the F_2 and back-cross generations. When, however, we compare skewnesses (Table XII), large discrepancies appear. In the first place many families in Table XII show a very low value for the skewness of the arithmetic distributions. In only six families is the skewness as large as three times the probable error. As might be expected, the families with very low skewness in arithmetic distribution show a higher value for skewness in logarithmic distributions. Such are the distributions in families number 25.21, 25.22, 25.32, 25.40, 25.45, and 25.58. Of these 25.32 and 25.40 exceed three times their probable errors and are presumably significant, i.e. not due to errors in sampling.

Interpretation of the Data

The regularity with which the pepper data give unimodal distributions in the F_2 , the back-crosses and the second generation after the back-crosses, indicates that the length of the fruit is determined by a large number of genetic factors. The skewness of the arithmetic distributions of the F_2 and back-crosses is found to be greater than three times the probable errors, while the logarithmic distributions of these generations give normal curves. This is the expected behavior for quantitative factors

TABLE X

VARIATION IN MEAN FRUIT-LENGTHS (20 FRUITS PER PLANT)
IN FAMILIES OF SECOND SELFED GENERATION AFTER
BACK-CROSS BETWEEN CORAL GEM AND F₁

Family number	Class values in mm.													
	13-17	18-22	23-27	28-32	33-37	38-42	43-47	48-52	53-57	58-62	63-67	68-72	73-77	78-82
25.5		8	21	18	6	3								
25.8		10	20	21	10	3	2							
25.18			4	1	21	16	17	12	7	3	1			
25.20		1	1	10	22	20	12	4						
25.21		1	5	6	12	17	16	12	6	4	1			
25.22		1	10	13	29	15	7	4						
25.24		1	4	6	11	10	4	4	0	0	1			
25.25	1	7	17	38	31	12	6	3						
25.26		2	21	16	6	1								
25.30			1	6	12	24	28	29	14	9	7	2	1	1
25.31		1	6	9	7	13	5	1	0	1				
25.32		1	1	10	9	12	21	19	9	4	4	1		
25.33		7	50	51	2	1								
25.34	1	12	31	16	2	1								
25.40			6	7	25	14	25	14	5	3	1			
25.42			12	19	41	36	40	27	24	11	6	0	4	1
25.43		4	12	25	28	26	13	9	4	2				
25.44		3	19	30	19	14	9	1						
25.45		9	27	40	43	15	1							
25.46		3	27	22	20	5								
25.48			7	12	19	15	6	0	2					
25.51		5	12	26	31	22	6	1	1	3				
25.52		2	14	14	13	9	5	3	3					
25.58		1	5	13	22	11	11	5						
25.64			3	13	17	12	10	7	4					
25.71			7	21	28	22	8	3	2	1	1			
25.83II		4	30	47	24	6								
25.84		4	23	21	9	2								

TABLE XI

LOGARITHMIC DISTRIBUTIONS OF MEAN FRUIT-LENGTHS (20
FRUITS PER PLANT) IN FAMILIES OF SECOND SELFED
GENERATION AFTER BACK-CROSS BETWEEN CORAL
GEM AND F₁

Width of logarithmic classes 0.05

Family number	Class value in mm.														
	15.8-17.7	17.8-19.8	19.9-22.3	22.4-25.0	25.1-28.1	28.2-31.5	31.6-35.4	35.5-39.7	39.8-44.6	44.7-50.0	50.1-56.1	56.2-63.0	63.1-70.7	70.8-79.3	79.4-89.0
25.5		1	7	12	13	11	7	4	1						
25.8		1	9	16	13	9	9	5	3	1					
25.18				2	2	1	10	20	14	19	9	4	1		
25.20			1	1	0	7	16	22	10	11	2				
25.21			1	1	4	4	9	15	13	17	10	6			
25.22			1	5	8	5	21	20	9	10					
25.24				1	5	4	3	11	9	7	0	1			
25.25		1	1	6	11	14	29	22	15	10	4	2			
25.26			2	6	17	13	5	3							
25.30					2	4	8	17	21	37	23	15	5	1	1
25.31			1	4	3	6	8	8	7	5	0	1			
25.32			1	0	3	5	9	7	20	24	11	8	3		
25.33			7	26	37	34	6	0	1						
25.34	1	1	11	20	19	7	2	2							
25.40				3	5	4	12	22	18	23	9	3	1		
25.42				2	11	12	28	30	42	38	33	15	5	5	
25.43		1	3	2	14	16	25	23	18	12	7	2			
25.44			3	7	18	17	20	12	13	5					
25.45			9	12	26	20	38	21	7						
25.46			3	14	20	11	15	11	3						
25.48				3	7	7	11	20	8	3	2				
25.51			5	6	11	13	27	21	16	4	1	3			
25.52			2	5	12	11	6	13	5	5	4				
25.58			1	1	5	6	20	15	10	8	2				
25.64				1	4	5	17	10	13	9	6	1			
25.71				1	9	15	19	22	17	6	2	1	1		
25.83II			4	16	24	30	24	12	1						
25.84			4	10	19	12	10	2	2						

TABLE XII

SKEWNESS OF ARITHMETIC AND LOGARITHMIC
DISTRIBUTIONS IN FAMILIES OF SECOND SELFED
GENERATION AFTER BACK-CROSS BETWEEN
CORAL GEM AND F_1

Family number	Number of individuals	Skewness		
		Equal-size classes	Logarithmic classes	Probable error *
25.5	56	.49	.26	± .22
25.8	66	.59	.51	± .20
25.18	82	.21	-.37	± .18
25.20	70	-.17	-.43	± .20
25.21	80	.00	-.51	± .18
25.22	79	.17	-.39	± .19
25.24	41	.61	-.32	± .26
25.25	115	.32	-.05	± .15
25.26	46	.57	.21	± .24
25.30	134	.54	-.17	± .14
25.31	43	.40	-.14	± .25
25.32	91	.03	-.55	± .17
25.33	111	.15	.22	± .16
25.34	63	.44	.35	± .21
25.40	100	.18	-.57	± .17
25.42	221	.58	-.06	± .11
25.43	123	.40	-.12	± .15
25.44	95	.38	.05	± .17
25.45	135	-.14	-.29	± .14
25.46	77	.23	.18	± .19
25.48	61	.51	-.15	± .21
25.51	107	.83	-.01	± .16
25.52	63	.65	.22	± .21
25.58	68	.11	-.23	± .20
25.64	66	.36	-.03	± .20
25.71	93	1.07	.39	± .17
25.83 II	111	.17	-.07	± .16
25.84	59	.38	.39	± .22

* The formula $E\alpha_3 = 0.6745 \sqrt{\frac{6}{n}}$ was used in the calculation of probable error.

if the factors have proportionate effects and if there is no dominance, or if any dominance of factors in one direction is offset by equal dominance of other factors in the opposite direction. Since the F_2 and back-crosses represent random distributions of the factors, it is assumed that there would be no disturbing effect of dominance. The statistical analysis thus agrees with the theory of proportionate effects of the factors.

The irregularity of skewness in the second generation after back-crossing contrasts strongly with the skewness of the F_2 and back-cross generations. The difference appears to be due to dominance resulting from the fact that there is not a random distribution of the factors in the second generation after the back-crosses. The skewnesses of Table XII are, however, not all equally significant because of the smallness of some of the families and the limited range of others. Nevertheless, the fact that all but 2 of the arithmetic distributions show positive skewness, while the logarithmic distributions show 10 positive and 18 negative, is compatible with the theory of proportionate effects.

GENERAL DISCUSSION

Factorial Interactions and Quantitative Inheritance

Examination of the literature shows various types of factorial interactions which bear on the inheritance of quantitative characters.

Bridges (1919), in a study of eosin eye color in *Drosophila*, found eight recessive modifying factors each of which in a double homozygous combination with eosin produced a specific modification of the eosin character. The types of modification resulting from the interaction of these modifiers and the eosin factor were as follows: (1) general modifications in which the combination of eosin and a modifier had a cumulative effect, each factor having a more or less proportionate influence; (2) specific modifications (the most common type) in which the modifier had no visible effect except in the presence of eosin, the combination giving a much lighter type than eosin; (3) disproportionate modifications in which the modifier alone had only a slight effect, but in combination with eosin had a very pronounced effect; and (4) re-

versed modification in which the modifier alone produced a darker eye color than wild-type, but in combination with eosin produced an eye color lighter than the eosin.

Emerson (1918) shows that three dominant factors, *A*, *C*, and *R*, are necessary to the production of aleurone color in maize. The fact that all three dominant factors must be present made it possible to segregate out "aleurone testers" in which one factor was kept in a recessive condition and the other two in the dominant condition. Such a type furnished a simple means of testing for the presence of the third dominant in an unknown stock.

Emerson and Emerson (1922) describe two dwarf types of maize, anther ear and dwarf, of which the double recessive dwarf anther ear was disproportionately small. Anther ear was about three fourths of the normal in height while dwarf was approximately one fourth of normal. The double recessive dwarf anther ear was about one sixteenth as tall as the normal.

Equality of the Factors

Nilsson-Ehle (1908) found that red color in wheat (*Triticum vulgare*) was due to three apparently equal dominant factors which were cumulative in their effects. Such factors are known as duplicate factors. Subsequently to Nilsson-Ehle's work several cases involving two duplicate factors were worked out. Of these the inheritance of capsule form in *Capsella* (Shull, 1914) is perhaps best known. A number of additional cases of duplicate factors have been found in wheat and oats and, as recent cytological work has shown, polyploid series occur in both these forms. For example, Sax (1921) has shown that common wheat is a hexaploid (42-chromosome) form and it seems very probable that the three-factor series for red color represents a threefold replication of a single pair of chromosomes, each carrying a factor for red color. There are, however, a few cases which cannot be explained in this way.

In spite of the rare occurrence of duplicate factors which was pointed out by Shull (1914), the impression grew up that quantitative characters were in the main determined by factors which were equal and independent in their effects. Castle's formula

(1921) for the determination of the number of factors in blending inheritance is an example of this. It is to be expected that duplicate factors would be found chiefly in forms belonging to polyploid series. They play only a minor part in the simpler types of inheritance and there is no reason to suppose they play a more important part in complex types of quantitative inheritance.

Dominance

Crosses involving quantitative characters usually give an F_1 which is intermediate between the parents. Dominance is either incomplete or not apparent and the result is often called blending inheritance. But it occasionally happens, as in the case of crossing inbred races of corn, that such a cross gives very greatly increased size and vigor in the F_1 . Such an effect has been called vigor of heterozygosis, or "heterosis." Jones (1917) suggested that this increased growth is due to the number of dominant factors brought together in the F_1 and this explanation is now generally accepted.

Proportional versus Additive Effects

Both Zeleny's data and the pepper data furnish strong presumption in favor of the theory of proportionate effects of the factors. It is clearly impossible to explain the pepper data on the theory of absolute or additive effects. There is, furthermore, a priori support for the theory of proportionate effects in that (1) growth phenomena tend to be of a geometric order and (2), as Zeleny (1922) pointed out, quantitative data very commonly show positive skewness.

Multiple-factor Expectations from Simple Cases

There is no obvious difference between the genetic behavior of quantitative characters and a synthetic multiple-factor situation such as could be built up from a combination of non-allelomorphic factors all affecting a single character. In *Drosophila*, for example, the color of the eye is affected by a large number of factors. The F_2 generation of a cross between a normal red-eyed fly and one homozygous for the six factors, eosin, vermilion,

purple, purploid, peach and claret, would almost certainly baffle any attempt at genetic analysis. It could, in fact, be used as a typical case of quantitative inheritance.

Manglesdorf (1926) gives a list of eighteen factors affecting the development of endosperm in maize. Some of the factors affect primarily the texture of the endosperm, while others affect the amount of endosperm produced. There does not appear, however, to be any fundamental difference between these characters. The amount of deficiency varies with the different factors and Manglesdorf has calculated the percentage in each case. All the factors behave as simple recessives. A cross between normal starchy endosperm and an individual homozygous for any six or more of the defective endosperm factors taken at random would be expected to give an F_2 distribution typical in all respects of quantitative inheritance.

Behavior of the Factors in Quantitative Inheritance

As a rule the data of quantitative inheritance are, in a critical sense, unanalyzable. Any conclusions as to the factors for quantitative characters must be based upon the known facts of normal genetic behavior. We might expect dominance (partial or complete), recessiveness, equality or inequality of the factors, modifying factors, linkage and crossing-over. It is an interesting fact that a most improbable assumption, that of the equality of factors, has played a large part in the study of quantitative inheritance. The demonstrated cases of duplicate factors indicate that they are so rare as to be negligible, except in polyploids. There is no warrant for supposing that, aside from the cases of duplicate factors, equality of the factors occurs except as a result of coincidence.

It can hardly be doubted that in the inheritance of quantitative characters all degrees of dominance and recessiveness occur. So thoroughgoing a demonstration of modifying factors as Bridges (1919) has given in the case of modifiers of eosin eye-color in *Drosophila* indicates that factors of this type may be widespread, and that they may explain, as Bridges believes, the results of selection experiments. Moreover, the whole bulk of the Droso-

phila work points to the fact that all characters, if sufficiently analyzed, show the effect of many genetic factors.

SUMMARY

Inheritance of fruit-length was studied in a cross between Coral Gem pepper with a mean fruit-length of 23.2 mm. and Anaheim with a mean length of 156.9 mm.

The data of the F_2 and back-cross generations in logarithmic classes gave normal curves and in arithmetic classes gave skewed curves. This indicates that the factors for length have proportionate rather than additive effects.

Skewness was irregular in the second generation after the back-crosses.

A general discussion of the interpretation of quantitative inheritance is given.

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